

RECONSTRUCTION OF THE JAWS AND BRAINCASE IN THE DEVONIAN PLACODERM FISH *BOTHRIOLEPIS*

by G. C. YOUNG

ABSTRACT. New material of the antiarch *Bothriolepis*, from the Gogo Formation (early Upper Devonian, Canning Basin, Western Australia), provides morphological details of the visceral jaw elements, which were not previously known in antiarchs. The palatoquadrate lacks a high orbital process, and was attached to the ventral part only of the suborbital (mental) plate. This shows that the ethmoidal region of the braincase must have been considerably deeper than previously thought. Detailed descriptions are given of the dermal elements in the jaws (suborbital and infragnathal) and cheek (submarginal, prelateral, infraprelateral). On the evidence of the palatoquadrate the mental plate of antiarchs is homologized with the suborbital in other placoderms. The absence of supragnathals may be secondary, and the differentiation of the infragnathal into biting and non-biting divisions probably evolved independently in antiarchs and euarthrodires. Reassembly shows that the submarginal and infraprelateral plates in *Bothriolepis* fitted closely against the anterior ventrolateral to close the operculum. A new restoration of the endocranium is presented, based on the identification of a posterior postorbital process and cucullaris fossa in *Asterolepis*. It is suggested that in *Bothriolepis* the palatoquadrate had an amphistylic connection to subocular and subnasal shelves, that the lateral pit was bounded posteriorly by the anterior postorbital process to form a mandibular muscle fossa, and that the preorbital recess housed the rhinocapsular bone. Comparison with *Yunnanolepis* indicates that the preorbital depression in this form contained a discrete rostral capsule with lateral nasal openings, and that the 'orbital fenestra' in those antiarchs with a preorbital depression is equivalent to the suborbital fenestra of *Bothriolepis*. Certain characters defining the relationships of antiarchs to other placoderm groups are summarized in cladogram form; prelaterals, infraprelaterals, a long obstatic margin, and prominent posterolateral corners on the skull are proposed as synapomorphies of antiarchs and euarthrodires. Fusion of the quadrate to the postsuborbital is a possible additional synapomorphy of actinolepids and phlyctaenioids.

THE remarkable preservation of fishes from the Frasnian (early Upper Devonian) Gogo Formation in the Canning Basin of north-western Australia is now well known through the publications of Miles (1971, 1977), Gardiner and Bartram (1977), Miles and Young (1977), Miles and Dennis (1979), and Dennis and Miles (1979a, b; 1980–1983). A preliminary faunal list and brief comments on the occurrence of this diverse fish fauna was presented by Gardiner and Miles (1975). The new information on the structure of the placoderm *Bothriolepis* presented here is based on material from a large collection of Gogo fish specimens made in 1972 by the Bureau of Mineral Resources and the Geological Survey of Western Australia. *Bothriolepis* is a well-known member of the highly specialized placoderm order Antiarcha, which had a cosmopolitan distribution during the Late Devonian, typically in non-marine sediments. Over fifty named species have been referred to the genus (e.g. Denison 1978). However, the occurrence of *Bothriolepis* in strictly marine calcareous sediments, as is the case with the Gogo fish fauna, is very uncommon. The mode of preservation in the Gogo material (whole fish in calcareous nodules) has permitted preparation using acetic acid techniques as developed by Toombs (1948) and Toombs and Rixon (1959), to reveal in intricate detail the skeletal morphology of this form. This new information largely confirms, but also supplements and enlarges upon, the comprehensive previous accounts of the morphology of *Bothriolepis* (see Stensiö 1931, 1948).

Many prepared specimens of *Bothriolepis* from the Gogo Formation are held in the British Museum (Natural History) and will be described in a forthcoming account as a new species by Dr.

R. S. Miles. The new information on jaw and braincase structure described here is based on a single specimen in which delicate and extremely fragile surface (perichondral) ossifications of various cartilaginous elements were recognized during preparation. These structures have not previously been identified in *Bothriolepis*, in which the braincase and gill arches were predominantly cartilaginous. The material described below is housed in the Commonwealth Palaeontological Collection (prefix CPC) in the Bureau of Mineral Resources, Geology and Geophysics, Canberra. The terms 'interperichondral space', 'closed margin', and 'open margin' are used in the description of perichondrally ossified elements as defined by Miles and Young (1977, p. 145). The following terms for dermal bones of the cheek region are substituted for those previously applied to antiarchs: submarginal for extralateral, and suborbital for mental plate. Evidence for establishing these homologies is presented below.

MATERIAL

The specimen (CPC 25205) on which this study is based includes the three major cheek bones (submarginals, infraprelaterals, and the left prelaterals), upper and lower dermal jaw elements from both sides, a possible extramandibular plate, both palatoquadrates, and the left Meckel's cartilage, the latter elements attached to their respective dermal bones. The nuchal plate is missing from the skull-roof, but the complete anterior region of the skull together with the well-preserved and articulated ventral trunk armour has enabled the space containing the orobranchial cavity to be delineated by direct reassembly of the specimen.

DESCRIPTION

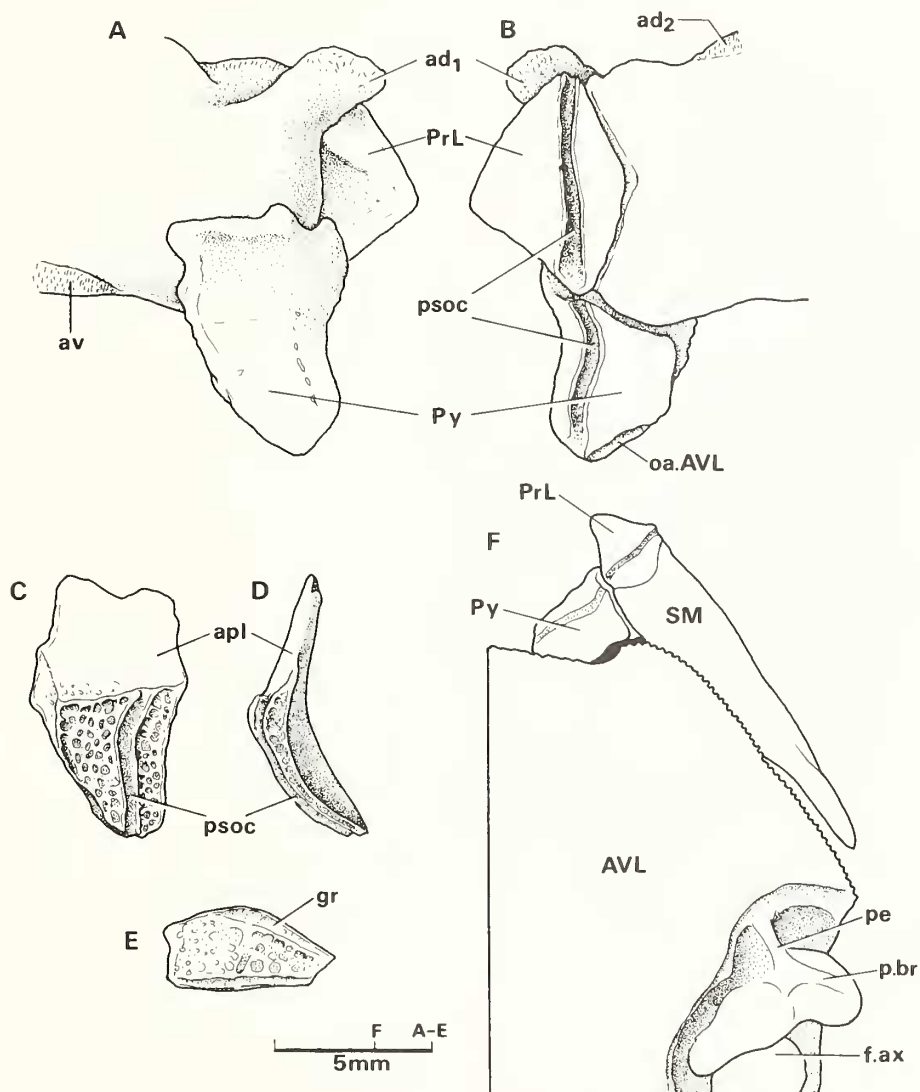
1. *Dermal elements of the jaws and cheek.* Because of their excellent preservation these bones provide several new morphological details not previously covered in Stensiö's comprehensive descriptions (1931, 1948).

The suborbital (mental) plate, which is the upper dermal jaw element, is shown in external view in Pl. 58, fig. 1. In shape it corresponds well with this bone in *B. canadensis*, but the lateral notch is more pronounced, with a longer posterior process (p.pr, text-fig. 2), and the posterodorsal corner is less marked, as in *B. cellulosa* or *Grossilepis* (Stensiö 1948, fig. 35). The external surface is ornamented in its dorsal part, with a broad strip of smooth bone along the denticulated ventral margin. Stensiö regarded these as distinct 'tooth' and 'sensory canal' components of a compound bone, but this seems unlikely. The shallow groove (gr.ul, text-figs. 2, 3) separating these two regions probably housed soft tissue forming an upper lip. The infraorbital sensory groove (ifc) crosses the bone in a similar fashion to that of other antiarchs.

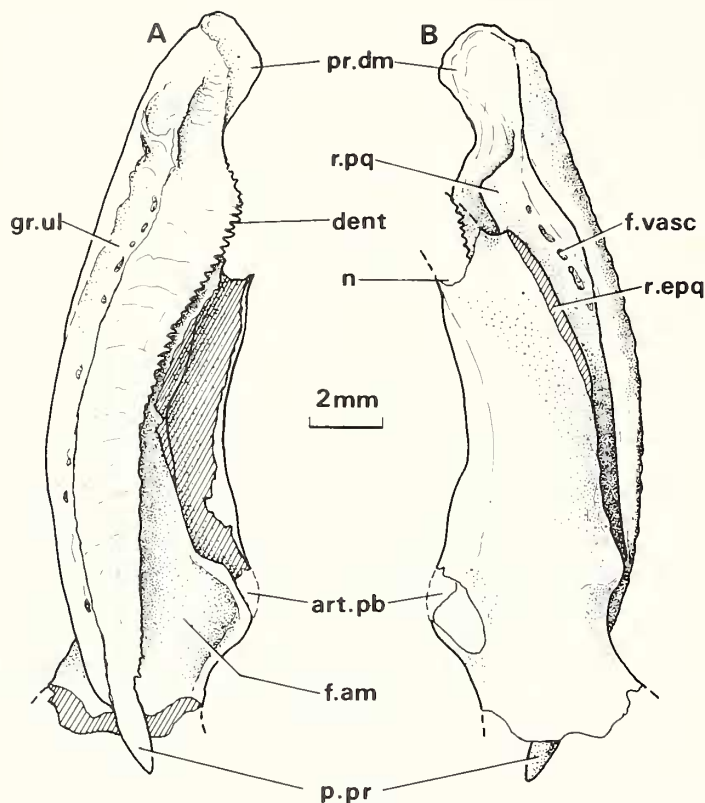
On the inner surface of the plate is a distinct ridge (r.pq), as previously noted in *B. canadensis* (Stensiö 1931, 1948). Posteriorly it forms an inconspicuous thickening, but anteriorly it is well developed to support the palatoquadrate (text-fig. 3D, E), with its concave upper surface forming a shallow groove pierced by several foramina (f.vasc, text-fig. 2B). In both specimens the anterior end of this ridge is clearly seen in front of the broken perichondral lining of the palatoquadrate (Pl. 59). The groove-like upper surface of the ridge may correspond to the 'neurovascular groove' in *Holonema* (Miles 1971, p. 135), although at least some of its contained foramina appear to open externally into the groove (gr.ul) delineating the biting portion of the bone on the outer surface. In its relationship to the palatoquadrate this ridge might be thought to correspond to the suborbital crista on the suborbital plate in brachythoracid euarthrodires (e.g. Miles and Westoll 1968, fig. 13), but the possibility that the adductor mandibulae musculature may have passed above it (see below) argues against this comparison.

A final structure of note is the rounded inner projection just beneath the anterodorsal corner of the plate (pr.dm, text-figs. 2, 3, 5). This forms a narrow flattened area on the anterior (mesial) margin, facing towards the symphyseal plane with the suborbital in position against the skull. It may have been an attachment site for an anterior ligamentous connection between the suborbital plates of each side.

The infragnathal (Pl. 58, figs. 2, 3) is, as previously noted (Stensiö 1931, 1948), made up of a posterior non-biting and an anterior biting division, as in some euarthrodires. Some new details can be added to previous descriptions of this bone. The presence of a denticulate biting margin on the anterior division (Stensiö 1931, p. 64) is confirmed. The posterior division is broader than the anterior, with fairly straight lateral and posteromesial margins, and a convex anteromesial margin.



TEXT-FIG. 1. (See list of Abbreviations used in Text-figures, p. 661.) *Bothriolepis* sp. CPC 25205. Gogo Formation, Canning Basin, Western Australia. A, left prelatral and infraprelateral plates reassembled against the anterior end of the left submarginal plate, visceral view. B, the same, in lateral view. C, D, right infraprelateral in lateral and anterior views respectively. E, possible right extramandibular plate, external view. F, reassembly of the left submarginal, prelatral, and infraprelateral plates against the anterior ventrolateral plate of the trunk-shield, ventral view.



TEXT-FIG. 2. *Bothriolepis* sp. CPC 25205. Gogo Formation, Canning Basin, Western Australia. Right sub-orbital plate with palatoquadrate attached, in ventral (A) and dorsal views (B).

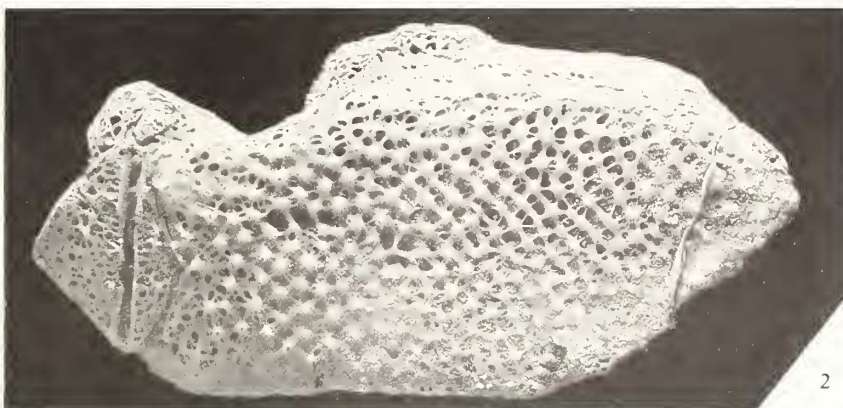
There is a prominent posterolateral corner (plc, text-fig. 5D). The dorsal surface is partly divided into mesial and lateral parts (mf,df) by a posterior continuation of the biting margin of the anterior division (dent). In these respects the bone closely resembles the infragnathal of *Grossilepis* (Stensiö 1948, fig. 36C-E). The ventral surface of the bone (Pl. 58, fig. 3) is concave over its whole length, where it was affixed to Meckel's cartilage (see below). Anteriorly this concavity forms a deep groove, giving way on the posterior non-biting division to a shallow depression flanked by low crests along the lateral and anteromesial margins. The posteromesial margin (pmm, text-fig. 5D) has a bevelled edge with a somewhat cancellous texture, and lacks a crest. Just inside this margin in both examples is a conspicuous groove (Pl. 58, fig. 3) for a nerve or vessel positioned between the cartilage and the dermal bone. This may correspond to the groove on the posterior division of the infragnathal in coccosteids (e.g. Dennis and Miles 1979a, fig. 14), where, however, it runs on the mesial surface of the bone.

EXPLANATION OF PLATE 57

Bothriolepis sp. CPC 25205. Gogo Formation, early Late Devonian, Canning Basin, Western Australia.

Fig. 1. Incomplete skull-roof in visceral view, with right submarginal plate attached, $\times 2$.

Figs. 2, 3. Left submarginal and prelateral plates in lateral and mesial views respectively, $\times 4$.



YOUNG, *Bothriolepis* from Gogo

Stensiö (1948, p. 96) suggested that the anterior and posterior divisions of the infragnathal in *Bothriolepis* lay respectively lateral and mesial to Meckel's cartilage, this being the same arrangement as in brachythoracid euarthrodires. It is clear from this new material that the infragnathal was positioned mainly dorsal to the cartilage element, but Stensiö's interpretation would still seem to be correct. On the anterior biting division the outer ventral crest delimiting the groove for the cartilage is much more pronounced (Pl. 58, fig. 3), and the reverse applies on the posterior division. In addition, the anterior and posterior divisions are twisted with respect to each other about the long axis of the bone, to accentuate this special morphological relation between dermal and cartilage elements.

Of the dermal cheek plates the prelateral is known only from the left side. In life it was closely attached to the submarginal (extralateral) plate (Pl. 57, figs. 2, 3). It is essentially a triangular bone, as in *B. cellulosa* (e.g. Stensiö 1948, fig. 31), and lacks the short dorsal margin seen in *B. canadensis*. However, it is proportionately higher and shorter in CPC 25205 than in the prelateral of *B. cellulosa*, although plate proportions are known to be somewhat variable in *B. canadensis*. Externally the bone is crossed by a sensory groove between its dorsal and ventral corners (psoc, text-fig. 1), presumably equivalent to the postsuborbital sensory canal of euarthrodires. The crest on the visceral surface beneath the sensory groove, previously known in *B. cellulosa*, is shown in this specimen to represent the anterior margin of the area in contact with the submarginal plate. The submarginal plate of the right side is shown in position against the skull-roof in Pl. 57, fig. 1. It makes two moveable attachments with the skull, the anterior connection in the form of a distinct anterodorsal process (ad₁, text-fig. 1), as in other species (e.g. Stensiö 1948, fig. 105). On both sides the ventral margin of the submarginal is thickened about half-way along its length and displays a flattened articular surface of spongy bone (av, text-figs. 1A, 9B) in a corresponding position to the ventral longitudinal crista in *B. canadensis* (Stensiö 1948, fig. 105c). Reassembly of the specimen shows that this surface abutted against a dorsally facing bevelled edge along the lateral margin of the subcephalic division of the anterior ventrolateral plate, immediately lateral to its anterolateral corner (text-fig. 1F). This would have effected a seal to the branchial chamber when the operculum was closed.

The infraprelateral plates, which are poorly known in other species, are excellently preserved in CPC 25205. As figured by Stensiö in *B. canadensis* (e.g. 1948, fig. 34), the ornamented part comprising the ventral division of this bone lies against the ventral border of both the submarginal and prelateral plates, and carries a continuation of the sensory groove from the latter plate. The unornamented lateral part of the plate (apl, text-fig. 1C, D) fitted inside the prelateral and submarginal plates in a loose attachment. The three plates from the left side are shown reassembled in text-fig. 1A, B. Also of interest is the way the infraprelateral fitted along the anterior margin of the anterior ventrolateral plate, immediately inside its anterolateral corner. Here a slight notch is developed, and a narrow overlap area on the posteromesial edge of the infraprelateral fitted loosely inside the anterior ventrolateral. Direct reassembly of the specimen suggests a small gap around the anterolateral corner of the anterior ventrolateral (text-fig. 1F), and it seems probable that the infraprelateral was carried in a flexible region of skin forming the floor of the branchial chamber. An associated thin dermal plate (text-fig. 1E) may be a right extramandibular, since it resembles this element as figured in *B. canadensis* by Stensiö (1948, fig. 110), and carries a groove along its presumed anterior margin which may have been a sensory canal or pit-line.

EXPLANATION OF PLATE 58

Bothriolepis sp. CPC 25205. Gogo Formation, early Late Devonian, Canning Basin, Western Australia.

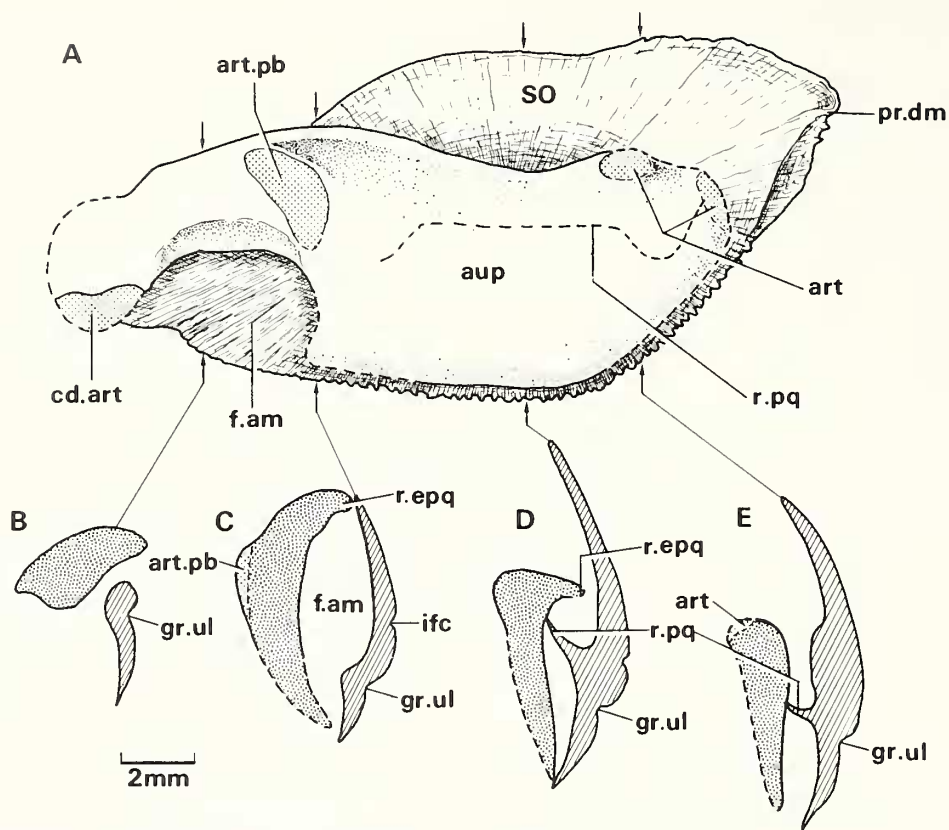
Fig. 1. External view of right suborbital plate with palatoquadrate attached, $\times 6$.

Fig. 2. Right infragnathal in dorsal view, $\times 6$.

Fig. 3. Left infragnathal in ventral view, $\times 6$.



YOUNG, *Bothriolepis* from Gogo



TEXT-FIG. 3. *Bothriolepis* sp. CPC 25205. Gogo Formation, Canning Basin, Western Australia. Restoration of the left suborbital plate and palatoquadrate. A, internal view (cf. Pl. 59, figs. 1, 2). B-E, sections at the levels indicated (dermal bone cross-hatched, cartilage stippled, articular surfaces with regular stipple).

2. *Palatoquadrate*. This element is similarly preserved on the inner side of each suborbital (mental) plate (Pl. 59, figs. 1, 2). Contrary to the reconstruction of Stensiö (1969, fig. 135), the palatoquadrate is long and low, and attaches mainly to the more ventral parts of the plate. Its closed dorsal margin lies just above the inner ridge (r.pq, text-fig. 3) in the central part of the plate. Posteriorly it curves slightly upward and over the lateral notch in the plate (Pl. 58, fig. 1). The autopalatine part of the palatoquadrate was relatively deep, its lateral (labial) perichondral surface extending and attached to the biting margin of the plate (text-fig. 3D). Exactly the same situation is seen in both plates, so any displacements between visceral and dermal elements can be discounted. The mesial (lingual) perichondral lining of this region is incomplete, but shows the autopalatine to have decreased in thickness ventrally. It is unlikely that the palatoquadrate would have projected past the biting margin of the suborbital, and it is assumed that it terminated here as a thin ventral border (text-figs. 3A, 5B). A similar situation is met with in *Holonema* and *Romundina* (Miles 1971, fig. 34; Ørvig 1975, pl. 2, fig. 5). The anteromesial extent of the palatoquadrate is not shown, but it is assumed that it formed an anterolateral connection with the braincase, as in other forms. The broken anterior edge of the outer perichondral lining curves away from the visceral surface of the suborbital at this level, and suggests an inward flexure of the palatoquadrate to form the orbital connection with the braincase. On both

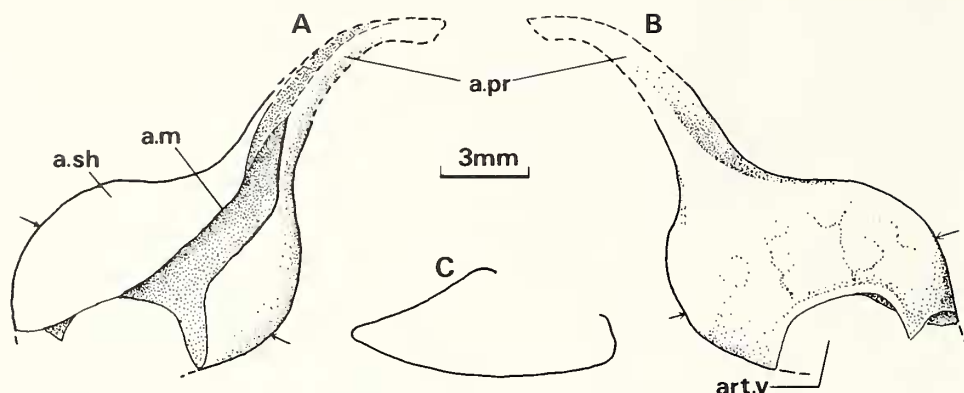
sides the anterodorsal edge of the perichondral lining is similarly preserved as a distinct notch (Pl. 59, figs. 1, 2; n, text-fig. 2B), which may have been the posterior border of an articular area (art, text-fig. 3A). However, this needs confirmation on better material, as it is not certain that this perichondral edge is a natural margin. Just behind the notch the dorsal margin of the palatoquadrate forms a laterally directed shelf (r.epq, text-fig. 3D), which extends posteriorly until it touches the suborbital plate at its dorsal margin (text-fig. 3C). At least on the right palatoquadrate this shelf has an open lateral margin (text-fig. 2B). This shelf delimits dorsally the space described below as an extension of the adductor fossa. As such it corresponds in position to the extra-palatoquadrate ridge in acanthodians or elasmobranchs (e.g. Miles 1973; Young 1982).

The metapterygoid region of the palatoquadrate is less deep but wider than the autopalatine, with a conspicuous dorsal flexure forming a ventral embayment, clearly the fossa for the adductor mandibulae musculature (f.am, text-fig. 3). Just in front of this fossa the palatoquadrate is separated from the suborbital ventrally, but is in contact dorsally. The inner ridge of the suborbital plate is reduced here to a low thickening, above which the concave inner surface of the suborbital and the concave outer (labial) surface of the palatoquadrate enclose a space in open communication ventrally with, and probably forming a dorsal extension of, the adductor fossa (f.am, text-fig. 3C). The dorsal-most opening through the perichondral lining, high on the lingual face above the adductor fossa, has slightly thickened rims showing it to be a natural opening representing another articular surface in contact with the endocranium (art.pb, text-fig. 3). The homologization of these various connections with the braincase amongst different placoderms is still uncertain. In *Romundina*, *Ctenurella*, and *Buchanosteus* there are three or more connections between the anterior portion of the palatoquadrate and the subocular shelf. The posterior two in *Buchanosteus*, by their close association with the groove for the efferent pseudobranchial artery, may be assumed to correspond, topographically at least, to the palatobasal connection in other fishes (Young 1979, p. 336). It is not clear how these correspond to the articular areas in *Romundina*, but in relation to the groove for the efferent pseudobranchial artery on the endocranium the posterior area labelled by Ørvig (1975, pl. 2, fig. 5) may correspond to the anterior part of the palatobasal connection in *Buchanosteus*, and another articular area may have been developed in the non-preserved part of the palatoquadrate immediately behind. This latter connection would have had an anterodorsal position relative to the adductor fossa, as with this posterior articular area in *Bothriolepis* (art.pb). However, in *Holonema* an articular area in much the same position was interpreted by Miles (1971) as for the orbital connection. In *Bothriolepis* a more anterior double orbital articulation has been restored after *Romundina* (art, text-fig. 3A), but it should be noted that in at least one euarthrodire (*Dicksonosteus*; see Goujet 1975) this was reduced to a single connection. In *Holonema* there were apparently no articular areas on the autopalatine corresponding to those of *Romundina* (Miles 1971, fig. 57).

At its lateral end the palatoquadrate of *Bothriolepis* is constricted, broader than high, and protrudes through the lateral notch in the suborbital plate (text-fig. 2), so that it lies above the posterior process (text-fig. 3B). The most posterior part of the ventral perichondral surface in both examples is inflected downwards, and this is interpreted as the edge of the condyle for the mandibular joint (cd.art). The more completely preserved palatoquadrate from the right side indicates that the condyle partly straddled and was in contact with the end of the posterior process of the suborbital plate.

In previous reconstructions of the palatoquadrate in *Bothriolepis* (Stensiö 1948, fig. 7; 1969, figs. 41, 42, 135; Miles 1971, fig. 112; Denison 1978, fig. 3) it has been depicted as a high short element somewhat similar to that of ptyctodontids, with a prominent orbital process extending dorsally to articulate with the endocranium beneath the orbital cavity. The closed dorsal margin of the perichondral lining in this new material shows this reconstruction to be incorrect. The palatoquadrate was low and long, without an orbital process, and occupied a position inside the ventral part only of the suborbital plate.

3. *Meckel's cartilage*. The posterior portion of this element was identified attached to the non-biting posterior division of the left infragnathal, from which it was subsequently detached (Pl. 59, figs. 3, 4). It is a fairly flat broad element which was fixed to the ventral surface of the posterior



TEXT-FIG. 4. *Bothriolepis* sp. CPC 25205. Gogo Formation, Canning Basin, Western Australia. Posterior part of left Meckel's cartilage (cf. Pl. 59, figs. 3, 4). A, dorsal view, showing flat surface affixed to posterior non-biting division of the infragnathal. B, ventral view. C, section through level indicated by arrows.

division of the infragnathal as oriented in text-fig. 4A. A dorsal view of the detached element (Pl. 59, fig. 3) shows clearly the area in contact with the dermal bone as a largely unossified region bounded anteriorly by a thickened perichondral margin (a.m, text-fig. 4A). As preserved, the area of contact corresponds closely in shape to the flat central region bounded by ridges on the ventral surface of the posterior non-biting division of the infragnathal (Pl. 58, fig. 3). There can be little doubt that a long narrow process of the cartilage (lost during preparation) extended to the extremity of the biting division of the infragnathal, in its ventral groove. The expanded posterior part of the cartilage projected anteriorly from beneath the infragnathal (a.sh, text-figs. 4A, 5D). This, together with the dorsolateral face of the non-biting division, probably formed the ventral area of attachment for the adductor mandibulae musculature.

The ventral surface of the preserved portion of the cartilage is completely ossified (text-fig. 4B, C), except for a deep embayment in its posterior margin (art.v), which has a slightly everted rim and was probably a cartilaginous articular surface. The function of such an articulation is uncertain, however, as it would have faced ventrally beneath the mandibular joint. It might correspond to the facet on the articular bone of ptyctodontids which may have received an element of the hyoid arch (Stensiö 1969, fig. 152; Miles and Young 1977, fig. 24). A similar facet is present also in brachythoracids, and was referred to by Stensiö (1963) as the 'supraglenoid area' (see Miles and Dennis 1979, p. 52). The mandibular articulation is not preserved in CPC 25205, but its likely position can be inferred from a consideration of the relationship between the upper and lower jaw elements (see below).

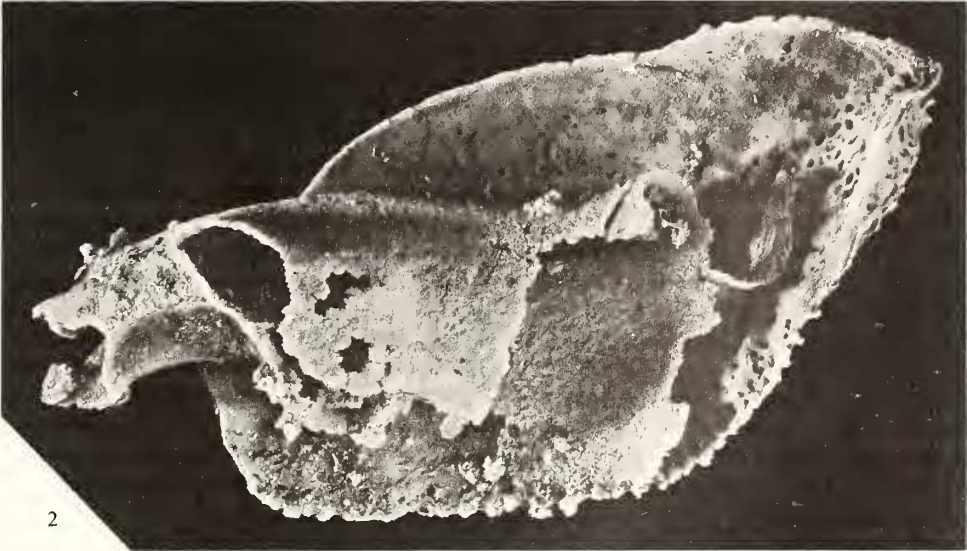
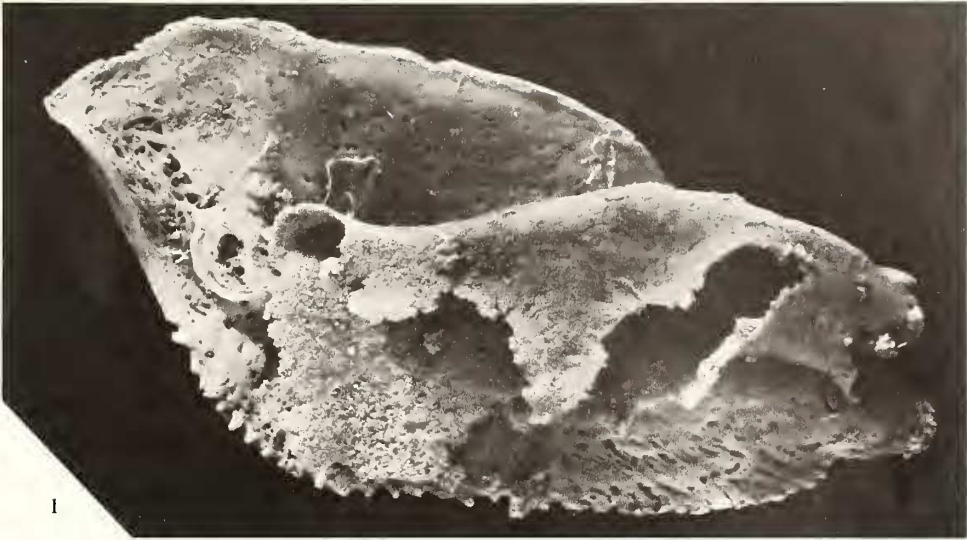
Again this element is much shorter and broader than restored by Stensiö (1948, 1969), and there is evidence that the mandibular joint was located adjacent to the posterior end of the infragnathal, and not some distance from it.

EXPLANATION OF PLATE 59

Bothriolepis sp. CPC 25205. Gogo Formation, early Late Devonian, Canning Basin, Western Australia.

Figs. 1, 2. Internal views of right and left suborbital plates with palatoquadrates attached, $\times 6$.

Figs. 3, 4. Posterior part of left Meckel's cartilage in dorsal and ventral views respectively, $\times 6$.



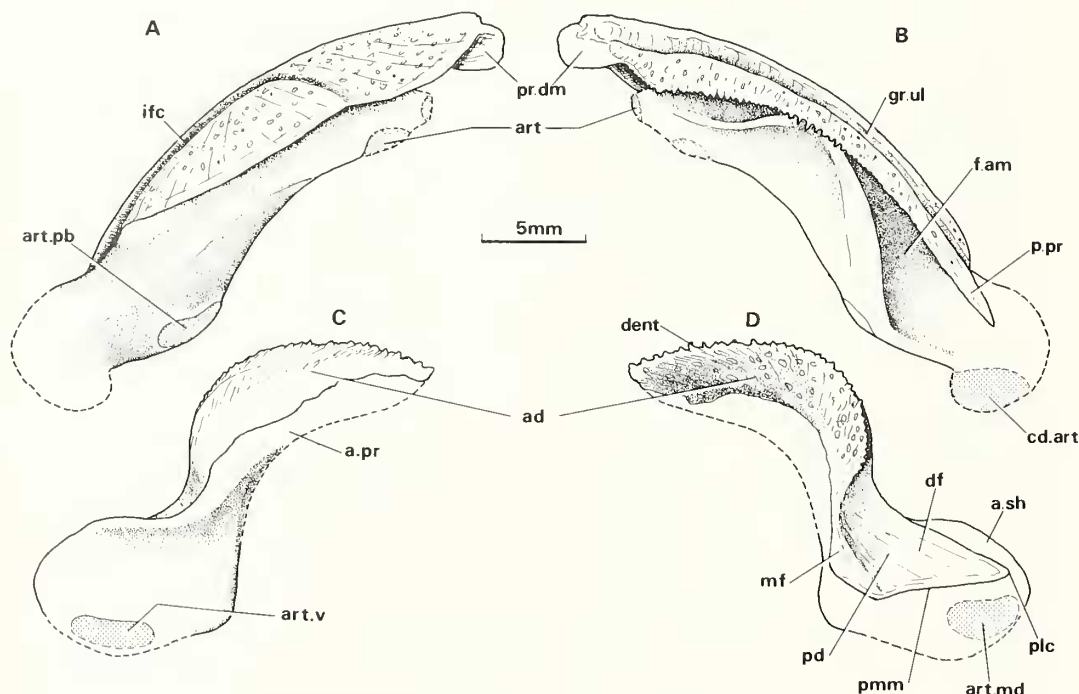
YOUNG, *Bothriolepis* from Gogo

RESTORATION

1. *Jaws*. A restoration of upper and lower dermal and visceral jaw elements in biting position is presented in text-fig. 5. The following constraints were applied in this restoration.

(a) Reassembly shows that the flat mesial edges of the suborbital plates do not fit against each other, indicating an intervening ligamentous or cartilaginous connection, as previously suggested for *Bothriolepis* (e.g. Stensiö 1948, 1969). As preserved (text-fig. 6) these plates lay symmetrically about the midline, but by fitting together the skull-roof and trunk armour and laying in the upper elements in the available space (see below) it became evident that they had been subject to post-mortem rotation. The configuration of the dorsal (anterior) margins of the suborbital plates in relation to the rostral margin of the skull-roof indicates a slight separation between left and right elements, as Stensiö concluded from a study of *B. canadensis* (1948, fig. 34).

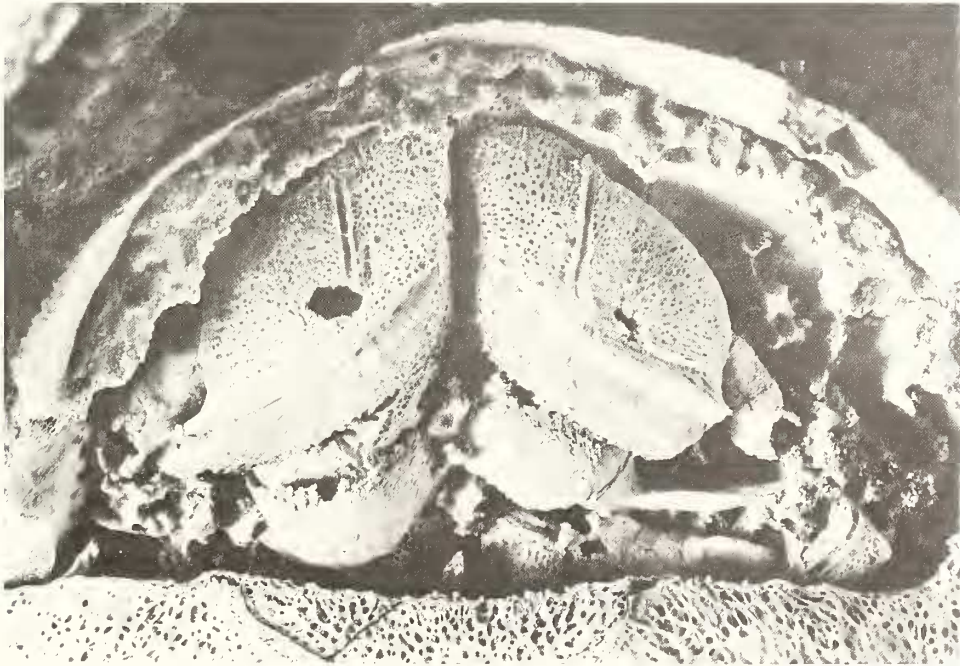
(b) By direct experimentation with upper and lower dermal elements their biting margins were oriented in presumed biting position, with the denticle rows subparallel. The biting margin of the infragnathal has much stronger curvature, and it is clear that it could not have closed outside the upper biting margin. It also seems unlikely that it bit inside this margin, because of obstruction by the palatoquadrate. It is possible, however, to place the jaw elements with good alignment between upper and lower denticle rows such that they occluded against each other. There is little freedom to adjust the two elements with respect to each other without the biting edges losing their alignment, so this is assumed to be a reasonable approximation of the correct biting position. Camera lucida drawings were prepared of each element in biting view.



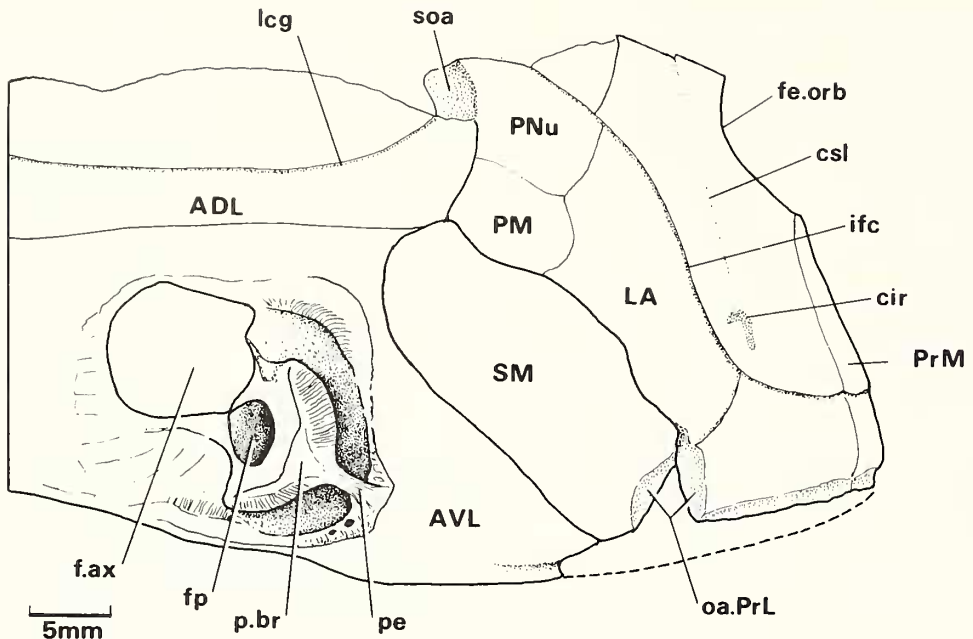
TEXT-FIG. 5. Restoration of jaw cartilages in *Bothriolepis*, after CPC 25205. A, dorsal view of a left suborbital and palatoquadrate, oriented as in B. B, ventral (occlusal) view of left suborbital and palatoquadrate. C, ventral view of right infragnathal and Meckel's cartilage, oriented as in D. D, dorsal (occlusal) view of right infragnathal and Meckel's cartilage.

(c) The likely position of the mandibular joint provides a third constraint on jaw position. As noted above, the posterior end of the palatoquadrate protrudes laterally to the posterior process of the suborbital plate. From the shape of the broken perichondral margins it is probable that the articular facet on the quadrate was immediately adjacent to the end of this dermal process, and the corresponding surface on the articular was immediately adjacent to the posteromesial margin of the posterior division of the infragnathal. To bring these surfaces together in the reconstruction the posterior division of the infragnathal needed a position as far lateral as possible, and it was necessary to assume some mesial flexure of the quadrate inside the posterior process of the suborbital plate. The restored position of the mandibular joint was determined both by superimposing outline drawings of the two elements, and by direct reassembly of the specimens. It should be noted that in this new restoration (text-fig. 5) the palatoquadrates are separated anteriorly, and do not form a symphysis (cf. Stensiö 1948, 1969). This is a primitive condition for placoderms at least (e.g. euarthroires, palaeacanthaspids, gemuendinids, petalichthyids), and probably also for gnathostomes (acanthodians, osteichthyans). The lower jaws of each side are also widely separated, but were possibly connected anteriorly by a median basimandibular, as restored by Stensiö (1969, fig. 135A). However, there is no preserved evidence in this material for the existence of this element.

The above procedure permits the reconstruction of upper and lower jaw elements with respect to each other, but gives no indication of their relationship to the skull-roof and endocranium. However, by reassembling the skull-roof against the trunk-shield the space available for the orobranchial cavity could be delimited. The submarginal and prelateral plates close in the gill chamber laterally, the former plate fitting closely against the anterior ventrolateral to effect an adequate seal with the operculum closed, as in other placoderms (e.g. Young 1980, fig. 18). As previously determined (Stensiö 1931, 1948) the mouth must have opened through that semicircular space delimited by the fairly straight leading ventral edge of the trunk-shield and the strongly curved rostral margin of the



TEXT-FIG. 6. *Bothriolepis* sp. CPC 25205. Gogo Formation, Canning Basin, Western Australia. Specimen in ventral view, partly prepared, to show preserved position of jaw elements, $\times 3$.



TEXT-FIG. 7. *Bothriolepis* sp. CPC 25205. Gogo Formation, Canning Basin, Western Australia. Right lateral view showing skull-roof reassembled against the trunk-shield. The dashed line from the leading ventral edge of the trunk-shield to the rostral margin of the skull-roof includes the assumed mouth position.

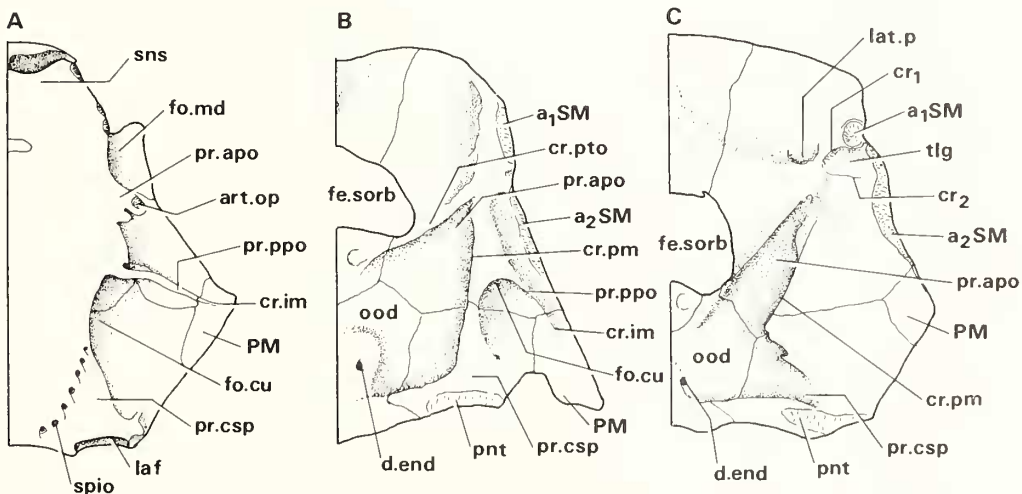
skull-roof. A lateral view of the reassembled Gogo specimen (text-fig. 7) confirms that this rostral margin and its lateral extremities lie in a slightly curved plane forming the anterior continuation of the flat ventral surface of the trunk-shield. The lack of angularities or projections in the overall conformation of the skull and trunk armours suggests that protruding jaws would have been most unlikely. As in previous restorations therefore (e.g. Stensiö 1948, 1969), it is assumed that the mouth was a transverse opening situated behind and slightly below the rostral margin of the skull-roof.

By suitably elevating the posterior part of the trunk-shield in CPC 25205 with the skull attached, it was possible to lay in the upper and lower jaw elements in their approximate positions on the flat surface supporting the specimen. At this angle the curved dorsal margins of the suborbital plates conform fairly well with the concave rostral margin of the skull-roof. The limited space available anterior to the anterior ventrolaterals shows that the upper jaws must have been carried adjacent to the rostral margin in a flap of skin. In this position it is clear that the mandibular joint must have been located approximately inside the prelateral plate, with the preserved dorsal articular surface (art.pb, text-fig. 3A) facing toward the lateral pit, but some distance below it. The palatoquadrate lies anteromesial to the articular process of the submarginal plate, the slope of its upper surface in the quadrate region conforming fairly well to the slope of the articular process. It is reasonable to suggest therefore that the epihyal fitted between these two structures. If the epihyal articulated against the anterior postorbital process of the endocranium, as it does in some other placoderms, then this process must have terminated approximately adjacent to the prelateral crista, and slightly above the anterior articular area for the submarginal. This assumes, of course, that the epihyal was neither attached to nor incorporated in the submarginal plate and its articular process.

2. *Endocranium*. The form of the palatoquadrate, as described above, demonstrates that the endocranium of *Bothriolepis* must have been much deeper than previously supposed, at least in its anterior parts, in order to effect an articulation with the palatoquadrate. The previous restoration of the endocranium by Stensiö (1948, figs. 6, 7; 1969, figs. 41, 42), largely followed by other workers (Miles 1971, fig. 112F; Denison 1978, fig. 3A), was based on the well-developed impressions for the dorsal surface of the endocranium on the visceral skull-roof surface in the region behind and lateral to the orbital fenestra (the 'otico-occipital depression' of Stensiö). Anteriorly little information is provided by the skull-roof, and here Stensiö relied on the assumption that the palatoquadrate was a short, deep element, with a prominent dorsal process which formed an orbital connection with the endocranium in a similar position, relative to the orbits, to this connection in other forms. To develop a new restoration of the braincase, based on the morphology of the palatoquadrate as described above, it is first necessary to consider the various endocranial processes in placoderms and their relations to visceral arch elements and associated muscles.

I have previously suggested (Young 1979, 1980) that there are grounds for homologizing most of the endocranial processes and associated fossae amongst the various major groups of placoderms, on the assumption that these structures were developed in different ways according to differences in the arrangement of the main muscles controlling movement of the cheek and jaws against the skull-roof and endocranium. By using these previously proposed homologies (text-fig. 8), and assuming constancy of morphological relations and function of corresponding endocranial structures in *Bothriolepis*, a new restoration of the endocranium has been prepared (text-fig. 9). The major changes in proportion resulting from dorsal migration of the orbits and nares, and the development of a prominent rostrum, appear to have had less effect on the posterior parts of the endocranium, where homologies to corresponding structures in other forms are fairly clear. These may be considered first, to establish a framework for interpreting the ethmoid and orbital regions.

The craniospinal process (pr.csp, text-fig. 8) in *Bothriolepis* supports the dermal neck-joint, and can be assumed homologous to this process in other placoderms as identified by Young (1980, fig. 24). The same process in Stensiö's restoration (1969, figs. 41, 42) was termed the 'supravagal process'. The supravagal process as redefined by Young (1980, p. 56) was apparently either extensively reduced or absent in *Bothriolepis*, as was the posterior postorbital process. However, there is evidence that in

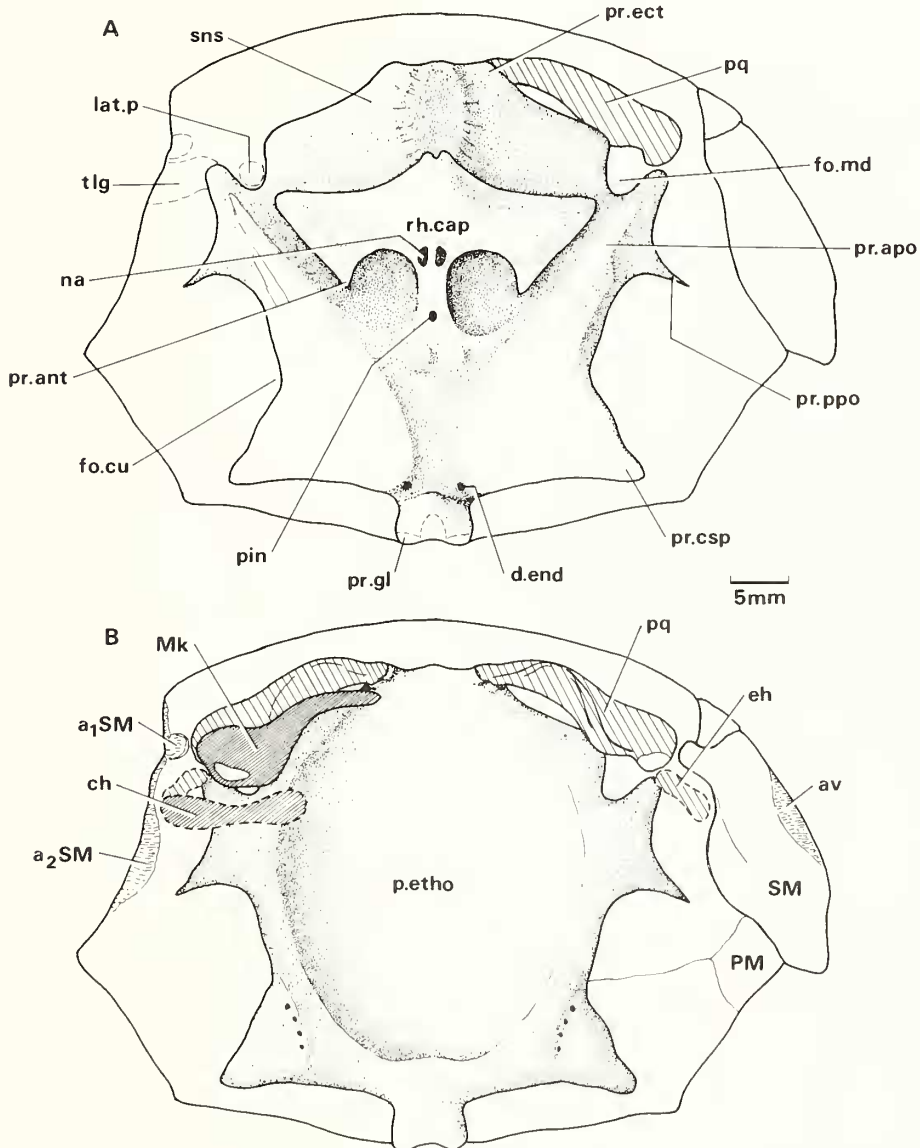


TEXT-FIG. 8. Endocranial processes in placoderms. A, ventral view of skull-roof and endocranium in *Bucanosteus* (after Young 1979, fig. 2). B, *Asterolepis*, skull-roof in ventral view (after Stensiö 1969, fig. 138C). C, *Bothriolepis*, skull-roof in ventral view (after CPC 25205). Not to scale.

some antiarchs the latter process was retained. A deep pit lying lateral to the paramarginal crista and opening posteriorly is known in *Asterolepis* (e.g. Stensiö 1948, fig. 17). This pit is bounded laterally by a crest of bone passing on to the postmarginal plate, which can be readily homologized with the inframarginal crista in euarthrodires such as *Coccosteus* (e.g. Miles and Westoll 1968). This homology is supported by the presence of a postmarginal sensory groove on the postmarginal plate in some primitive antiarchs (e.g. Zhang Miman 1980, pl. 1). In *Buchanosteus* the inframarginal crista (cr.im, text-fig. 8A) forms an extension to the posterior postorbital process, and marks the anterior boundary of the cucullaris fossa. Comparison with the visceral skull-roof surface in *Asterolepis* (e.g. Stensiö 1969, fig. 138c) indicates that this lateral pit, which faces posterolaterally toward the obstantic margin, also represents the cucullaris fossa (fo.cu, text-fig. 8B). Although there is no evidence that the posterior postorbital process was retained in *Bothriolepis*, a small process corresponding in position to that of *Asterolepis* is shown in the restoration (pr.ppo, text-fig. 9), to facilitate homologization of surrounding structures. However, there is good evidence of the shape of the dorsal aspect of the anterior postorbital process, which in *Bothriolepis* and other antiarchs must have occupied an anterolateral extension of the otico-occipital depression (pr.apo, text-fig. 8B, c). In most other placoderms this process carried one or two subterminal articular surfaces for visceral arch elements (palatoquadrate, epihyal, opercular cartilage). In *Asterolepis* the depression for this process lies adjacent to a dermal thickening which supported the connection and articulation of the submarginal plate against the skull-roof (a_1SM , a_2SM , text-fig. 8). In *Bothriolepis* there is a similar arrangement, although a more complex (apparently dermal) moveable articulation is developed between the articular process of the submarginal plate and the skull-roof. Whether the thickening supporting these articulations is entirely dermal in origin, or in fact represents the ossified terminal part of the anterior postorbital process, depends on the likely position of the epihyal element and its relationship to the submarginal plate. This is further considered below. In the restorations the anterior postorbital process is shown extending as far forward as the transverse lateral groove (tlg, text-fig. 9).

In *Buchanosteus* the subocular shelf formed a floor to the orbital cavity, and was continuous anteriorly with the subnasal shelf (sns, text-fig. 8A) which extended beneath the separately ossified rostral capsule (Young 1979). A similar arrangement is seen in *Romundina*, where the rostral capsule and nasal openings are dorsally placed (Ørvig 1975), and also in *Brindabellaspis*, where the two elements of the braincase show incipient fusion (Young 1980). The distribution of this character indicates that the separation of the endocranium into rhinocapsular and postethmo-occipital components was probably a primitive placoderm feature. Again, in both *Buchanosteus* and *Romundina* the palatoquadrate articulated against the lateral edge of the subocular shelf, or was closely held to it by ligaments, and this is also likely to be a primitive placoderm feature. In *Bothriolepis*, Stensiö (1969, figs. 41, 42) restored a high orbital process on the palatoquadrate, which articulated against the braincase in a dorsal position beneath the orbital fenestra, with the autopalatines of each side forming an anterior symphysis. However, as shown above, the palatoquadrate was low and broad, and it is clear that there must have been considerable anteroventral extension of the braincase to receive the palatoquadrate articulation. By comparison with *Buchanosteus*, and especially *Romundina* (in which the nares are dorsally placed), it can reasonably be assumed that the palatoquadrate retained its normal connection with subocular and subnasal shelves, even though the orbits and nasal openings had migrated dorsally to a mid-line position. In the restorations, therefore, three articulations between the palatoquadrate and subocular and subnasal shelves are shown: an anterior double articulation with an ectethmoid process, corresponding to the orbital connection known in *Kujdanowiaspis*, *Dicksonosteus*, *Ctenurella*, *Buchanosteus*, and probably *Romundina* (Stensiö 1963; Goujet 1975; Ørvig 1975; Miles and Young 1977; Young 1979); and a posterior single articulation, corresponding topographically to the palatobasal articulation, which is also known in *Buchanosteus* and probably *Romundina* (Young 1979, fig. 12; cf Ørvig 1975, pl. 1). To what extent the subocular and subnasal shelves of *Bothriolepis* were in contact with the visceral surface of the skull-roof is uncertain, but the poriferous area and associated ridges beneath the premedian plate (e.g. Stensiö 1948, fig. 15) suggest attachment in this region (the endocranial 'rostral

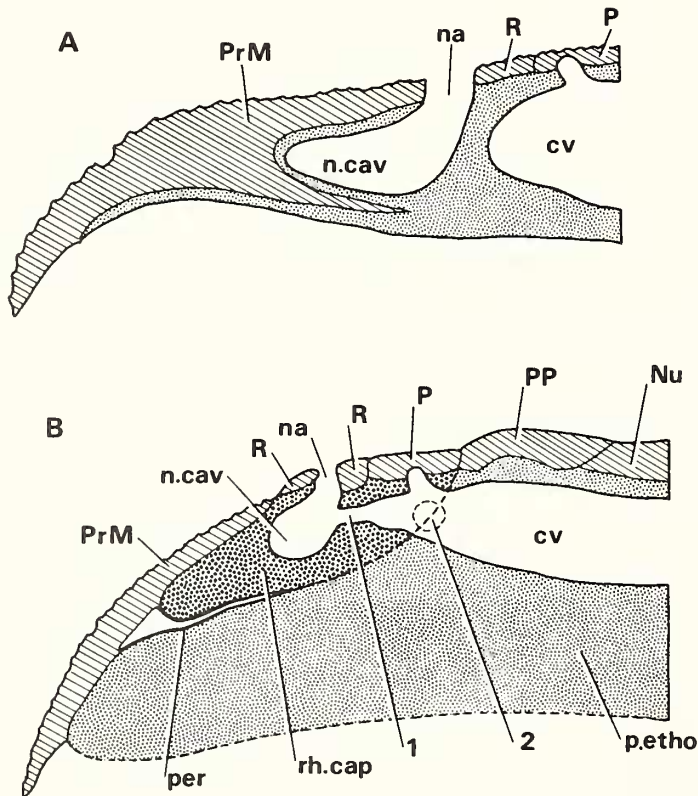
process' of Stensiö's restoration). The anterolateral corners of this rostral process in *B. canadensis* approximate in position to the ectethmoid processes restored here (pr.ect, text-fig. 9A). As such they are appropriately placed to have received the anterolateral ends of each palatoquadrate, with the jaws in their correct position.



TEXT-FIG. 9. Restoration of endocranium, mandibular and hyoid arch elements in *Bothriolepis*, Dermal skull-roof, and cheek plates of one side, shown in outline. A, dorsal view, with right palatoquadrate in approximate position (modified in part after Stensiö 1969, fig. 41). B, ventral view, with epihyal (unknown) and palatoquadrate in approximate positions. Position of right ceratohyal (unknown) and right Meckel's cartilage based on assumed position of palatoquadrate and epihyal.

Clearly there must have been muscles of mandibular derivation controlling movement of the palatoquadrate against the braincase, and in other forms (Young 1979, 1980) an embayment in the lateral endocranial wall, bounded posteriorly by the anterior postorbital process, has been proposed as the likely site of insertion of the m. levator palatoquadrati (fo.md, text-fig. 8A). In *Bothriolepis* the thickening on the lateral plate determined above as adjacent to or part of the anterior postorbital process, forms the posterior boundary of the lateral pit, which in this Gogo specimen (Pl. 57, fig. 1) is a distinct irregular depression readily interpreted as a site for muscle insertion. An embayment in the endocranial wall in this position, corresponding to the mandibular muscle fossa identified in *Buchanosteus* (Young 1979, fig. 2), is shown on the restorations (fo.md, text-fig. 9). It is possible, however, that this fossa was partly closed in ventrally by the subocular shelf.

The presence of extensive subocular and subnasal shelves in *Bothriolepis*, as is required to effect a connection with the palatoquadrate, leads to a new interpretation of the preorbital recess in this form. This structure, a backwardly opening cavity beneath the posterior part of the premedian plate, has been interpreted by Stensiö (1948, 1969) as a cartilage-lined space completely occupied by the nasal sacs (text-fig. 10A). The recess is floored by a lamina of bone projecting posteroventrally from the visceral surface of the premedian plate, and enclosed in cartilage under Stensiö's restoration. The shape of the recess amongst different species of *Bothriolepis* is well known (e.g. Stensiö 1948, figs. 13–15; Miles 1968, figs. 7, 43, 58), and there can be no doubt that the recess was either filled or



TEXT-FIG. 10. Paramedian sections through the preorbital region of the head in *Bothriolepis*. A, after Stensiö (1969, fig. 135B). B, new interpretation showing suggested position of rhinocapsular bone.

lined with cartilage. In view of the position of the preorbital recess in relation to the remainder of the braincase as restored here, I suggest that this structure was in fact the rhinocapsular bone of the endocranium (rh.cap, text-figs. 9A, 10B). Disregarding changes in proportion, it can be noted that this structure occupies the same position in relation to the subocular and subnasal shelves of *Kujdanowiaspis*, *Buchanosteus*, or *Romundina*, as does the rhinocapsular bone in these forms (Stensiö 1963; Ørvig 1975; Young 1979). The bony lamina forming the floor of the recess, and enclosed in cartilage under Stensiö's restoration (an anomalous relation if this lamina is of dermal origin), may be reinterpreted by comparison with *Brindabellaspis* (Young 1980, fig. 4). I suggest that it is a thickened remnant of a double perichondral layer representing contiguous surface ossifications of the two separate cartilages comprising the primitive braincase in placoderms. In *Brindabellaspis* this lamina is completely enclosed within the cartilage of the fused endocranium, and can be shown to have the correct morphological relations to surrounding nerves and vessels for it to represent the interface between rhinocapsular and postethmo-occipital portions of the endocranium. A similar interpretation for *Bothriolepis* presents no difficulty in relation to the optic nerve, which in other placoderms actually emanates between these two cartilages. Furthermore, the rhinocapsular bone thus delimited in *Bothriolepis* is attached to the rostral and pineal plates as in the other primitive placoderms mentioned above. The restoration shows posterolateral extensions of the rhinocapsular bone partly enclosing the orbits laterally, as do the antorbital processes in *Brindabellaspis* (Young 1980, fig. 8).

DISCUSSION

1. *Dermal bones of the jaws and cheek.* It is now evident that the so-called mental plate of antiarchs, a paired canal-bearing dermal bone forming the upper biting margin of the mouth, is homologous with the suborbital plate of other placoderms. This is confirmed by the fact that the palatoquadrate is attached to its inner margin. In view of the form of the palatoquadrate as demonstrated by this new material, any suggestion that the lateral plate incorporates homologues of the suborbital plate in whole or in part (e.g. Stensiö 1948, p. 200) may be discounted. On the other hand, the lower dermal jaw-bone in *Bothriolepis* includes differentiated blade and biting portions, as does the infragnathal in euarthroires, and might therefore be considered the homologue of this bone. If so, it could be suggested that the absence of any supragathal elements in *Bothriolepis* (and other antiarchs) is a secondary condition. This is consistent with assumed phylogenetic relationships of the antiarchs. However, there is other evidence indicating that the differentiated lower jaw-bone in antiarchs may have arisen within the group, in which case this argument would not apply. This is more fully considered below. Whether the antiarchs may have lost two pairs of supragathals is an interesting question, since Miles and Young (1977) proposed this as a synapomorphy of euarthroires. Further information on jaw structure in yunnanolepids may illuminate this point.

In advanced euarthroires the quadrate part of the palatoquadrate is fused inside the postsuborbital plate, although in primitive euarthroires and some other placoderms this plate is not readily recognized. In *Bothriolepis* both the prelateral and infraprelateral plates are canal-bearing bones lying adjacent to the mandibular joint, and one or both may represent a postsuborbital element which has either lost its close connection to the quadrate, or never had such a connection (see below).

Behind the suborbital-postsuborbital unit the operculum in placoderms is covered by a large dermal bone, the submarginal plate. In several groups this plate articulates with the endocranium through a cartilage fused to its inner surface. Again there is little doubt that the bone in antiarchs previously termed the extralateral plate is homologous to the submarginal (e.g. Miles 1971; Young 1980). In some asterolepidoids (e.g. Nilsson 1941) the plate carries a groove on its inner surface similar to the groove for the epihyal in phlyctaenioids (e.g. Goujet 1972, 1975), and in yunnanolepids the submarginal lies adjacent to a notch in the lateral skull-roof margin resembling the notch in a corresponding position in euarthroires (Zhang Miman 1980; Young 1980, p. 53). However, the development of a dermal articulation between the submarginal and the lateral plate in *Bothriolepis* is unique amongst placoderms, although an analogous articulation is seen between the suborbital and

postorbital plates in *Buchanosteus* (Young 1979). It is worth noting that this articulation in *Bothriolepis* is supported by a thickened ridge of bone beneath the lateral plate, interpreted above as being adjacent to, or part of, the anterior postorbital process. In euarthrodires the submarginal has an equivalent position, being connected to the endocranium through an articulation between the epihyal and the end of the anterior postorbital process.

2. *The preorbital recess and preorbital depression in antiarchs.* It has been suggested above that the preorbital recess of *Bothriolepis* housed the rhinocapsular bone of the endocranium, which was incompletely fused to the postethmo-occipital bone. In placoderms generally, the occurrence of a discrete rostral capsule in several distantly related groups indicates that this is a primitive placoderm feature (Young 1979, p. 341; 1980). It is of interest therefore that in the primitive yunnanolepid antiarchs from south China, and some other forms, the preorbital recess is not developed (Zhang Guorui 1978; Zhang Miman 1980). Instead, there is a broad dorsal depression in front of the orbital fenestra, recently interpreted by Janvier and Pan (1982) as the primitive condition for antiarchs, which was modified to form the recess of *Bothriolepis* and other more advanced forms by posterodorsal growth of the anterior border of the depression. This being so, one could suggest that the rostral capsule occupied the preorbital depression in yunnanolepids, and because it retained its primitive relation to the main portion of the endocranium as a discretely ossified unit, it is commonly lost and has largely gone unrecognized in these forms. In fact, remains of the rostral plate are known only in one specimen of *Yunnanolepis parvus*, as described by Zhang Miman (1980), who has, however, restored the nasal openings in a posterior position behind the preorbital depression and within the orbital fenestra. Consistent with this interpretation is the suggestion by Janvier and Pan (1982) that the preorbital depression in Yunnanolepiformes is homologous to the depression described by Ørvig (1975) on the 'median prerostral plate' of *Romundina*.

There are thus two alternative interpretations of the preorbital depression in primitive antiarchs. Under my interpretation of the preorbital recess in *Bothriolepis*, the preorbital depression is no more than a cavity which contained a discretely ossified rostral capsule in a position somewhat similar to that proposed by Zhang Guorui (1978). Under this interpretation the nasal capsules have a wholly dorsal position relative to the premedian plate. The alternative interpretation of Janvier and Pan (1982) proposes that the preorbital depression lies largely in front of and above the nasal capsules, and may be homologous to the depression in the dermal bone surface described by Ørvig (1975) as lying in front of the rostral capsule in *Romundina*. Under this interpretation the nasal capsules are ventrally situated relative to the premedian plate, perhaps extending forward on either side of the subpremedian ridge, as proposed by Zhang Miman (1980, p. 186).

In support of the second interpretation might be cited the fact that in *Y. parvus* the floor of the preorbital depression is ornamented, as is the depression on the prerostral plate in *Romundina*. But this raises a difficulty with Janvier and Pan's explanation of the fate of the depression in more advanced antiarchs, which requires that the ornamented (dermal) floor of the depression must have sunk into the endocranium to become enclosed in cartilage as the floor of the preorbital recess in bothriolepids. Similarly, the dermal ornament on the floor of the preorbital depression would appear to contradict my suggestion that the depression contained the rostral capsule, since under this interpretation the floor of the depression (like the floor of the preorbital recess in *Bothriolepis*) must be of perichondral derivation.

Since the preorbital depression in *Sinolepis* and *Microbrachius* is entirely lacking in ornament (Liu and Pan 1958; Hemmings 1978), the nature of the dermal tubercles in the preorbital depression of yunnanolepids is of particular interest. My observations on specimens in the Institute of Vertebrate Palaeontology and Paleoanthropology, Beijing, confirmed that in *Y. chii* the preorbital depression is smooth in the region of the premedian plate, but tuberculate in more lateral parts of the depression. The situation is less clear in *Y. parvus* because of its small size, but tubercles are again present in the lateral parts of the depression, and may extend towards the mid-line. The observation that these tubercles are much finer in the depression than on the surrounding bone surface indicates an explanation of their occurrence consistent with the interpretation of the preorbital recess in *Bothriolepis* presented above. I suggest that these fine tubercles surrounded the nasal openings, just as

very similar fine ornament is observed in the notch of the nasal opening in *Romundina* (Ørvig 1975), and *Buchanosteus* (e.g. Miles 1971, fig. 105). In *Yunnanolepis* the preorbital depression has groove-like lateral extensions, and I suggest that the nares opened laterally into these grooves. Any contact between the floor of the depression and the rhinocapsular bone of the endocranium would thus have been restricted to a narrow region of the mid-line. Under such circumstances dermal bone may grade imperceptibly into unornamented bone of perichondral derivation, as is the case in the rostral capsule of *Buchanosteus* (Miles 1971, p. 186). It should be noted that this interpretation is at variance with the conclusion of Zhang Guorui (1978, p. 154) that the nares in *Yunnanolepis* may have opened anteriorly, as in *Remigolepis*, and not laterally as in *Bothriolepis*, but there is also a phylogenetic argument supporting my view (see below).

A final point relates to the position of the nasal capsules in yunnanolepids and whether they may have been partly or wholly contained beneath the premedian plate on either side of the subpremedian ridge as proposed by Zhang Miman (1980). In *Y. chii* the so-called 'orbital fenestra' is a constricted oval-shaped opening facing anteriorly and somewhat dorsally into the preorbital depression. By comparison with the morphology of the orbital cavity as now known in some detail in other placoderms (e.g. Ørvig 1975; Young 1979, 1980) it can be suggested that the following nerves and vessels (all paired) must have gained access to the orbital cavity through this opening: optic (II), oculomotor (III), trochlearis (IV), profundus (V), and abducens (VI) nerves, the ophthalmica magna artery and possibly a branch of the orbital artery, and presumably an orbital or orbitonasal vein. In view of the small size of the 'orbital fenestra' in *Yunnanolepis* it seems inconceivable that the nasal capsules themselves could have been situated beneath it—this would require a similar position for the telencephalon of the brain, and a tortuous dorsal path for the optic nerves to reach the orbits, and of extensive nasal tubes to reach the nares. Considerations of space make it equally unlikely that the nasal capsules were positioned above the fenestra, through which the olfactory nerves passed in addition to those nerves and vessels just mentioned. In my opinion the only interpretation of the known structure of yunnanolepids and other antiarchs which is consistent with detailed endocranial morphology as known in other placoderms, is as follows: that the 'orbital fenestra' in various antiarchs with a preorbital depression is misnamed, being strictly homologous to the suborbital fenestra of *Bothriolepis*; and that the suborbital fenestra of antiarchs generally corresponds, at least in its dorsal parts, to the anterior fenestra of the endocranial cavity in forms like *Buchanosteus* (Young 1979, fig. 8), or *Romundina* (Ørvig 1975, pl. 2, fig. 2). As such, the equivalents of the crista supraethmoidalis in these forms, in antiarchs would have attached to the anterior edge of the postpineal plate, thereby marking the anterior limit of attachment of the postethmo-occipital bone of the endocranium to the dermal skull-roof. It is possible that the eye-stalk as known in other placoderms was secondarily lost in antiarchs. Vessels such as the orbital artery, which in other forms passed up through the suborbital shelf to reach the eyeball (e.g. Young 1980, fig. 10), must have entered the orbit through the ventral part of the suborbital fenestra.

3. *Phylogenetic implications.* The adoption of cladistic techniques in analysing phylogenetic relationships within the placoderms (e.g. Miles and Young 1977; Dennis and Miles 1979–1983; Miles and Dennis 1979; Young 1979, 1980, 1981b; Janvier and Pan 1982; Lelievre *et al.* 1982; Long 1983) has during the last few years generated a number of new ideas regarding placoderm evolution. These are testable in the sense that they make predictions about the morphology of various groups which can be checked as new information becomes available. An important aspect in this procedure is that any new morphological observation or interpretation of any taxon within the group under study is relevant to all other observations and interpretations of other taxa within the group. This results from the unifying character imparted to phylogenetic hypotheses by the use of cladistic techniques. With regard to antiarch phylogeny, an outline cladogram was presented by Young (1981a), and a more detailed proposal along similar lines was put forward by Janvier and Pan (1982). Interrelationships of antiarchs have been most recently discussed by Long (1983) and Young (in press), and relationships of antiarchs by Goujet (in press). In the context of these proposals, and more general schemes of placoderm interrelationships (e.g. Denison 1975, 1978; Miles and Young 1977; Young 1980), several ideas and observations developed above regarding the morphology of the head in *Bothriolepis* have

wider phylogenetic implications. These are the number of supragathal elements in the upper jaw, the differentiation of the infragathal into distinct blade and biting portions, the dermal articulation between the submarginal plate and the skull-roof, the relation between the quadrate and the postsuborbital plate, and the position of the nares in antiarchs. The phylogenetic arguments on each are briefly presented in points *a-e* below, and summarized in the cladogram of text-fig. 12.

(*a*) *Supragathals*. The suggestion by Miles and Young (1977) that two pairs of supragathals may be a synapomorphy of euarthroires predicts that other placoderm groups will have one or none of these elements. There are no supragathals in *Bothriolepis*, but a single pair has recently been reported in phyllolepis (Long, in press), which would mean that this was also the primitive condition in antiarchs, under the scheme of placoderm interrelationships proposed by Miles and Young (1977). Alternatively, the absence of supragathals in *Bothriolepis* can be seen as consistent with Goujet's (in press) view of antiarch relationships.

(*b*) *Infragathal*. Similarity between the infragathal of *Bothriolepis* and that of some euarthroires has been mentioned above. In a series of papers on brachythoracid euarthroires from Gogo (Dennis and Miles 1979*a, b*, 1980–1983; Miles and Dennis 1979), the differentiation of the infragathal into distinct posterior blade and anterior biting regions has been used as a synapomorphy of various brachythoracids (see also Young 1981*b*, fig. 17). This was based on the evidence that in *Holonema* the infragathal is not differentiated into two portions (Miles 1971), that in *Phlyctaenius* the few known infragathal remains (assumed by Heintz 1933 to be incompletely preserved) show only a biting region, and that various isolated denticulate bones from the early Devonian of Utah, also lacking a blade portion (Denison 1958, fig. 101), have been attributed to actinolepid euarthroires. In view of the specialized nature of the dentition in *Holonema* it is possible that the blade on the infragathal has been secondarily lost, and the evidence relating to *Phlyctaenius* is equivocal (e.g. Heintz 1933; Miles 1969). However, it seems reasonable on available evidence to attribute the isolated infragathals of Denison (1958) to the associated actinolepids, and it is noteworthy that the corresponding element in phyllolepis resembles these examples in general form (Long, in press).

Taking account of the differentiated infragathal in *Bothriolepis*, therefore, there are three alternative interpretations of the history of this element worthy of consideration, under an assumption that antiarchs and euarthroires are sister groups:

- (i) The differentiated infragathal was present in the common ancestor of antiarchs and euarthroires, and was secondarily lost in more primitive members (actinolepids, some phlyctaenioids) of the latter group.

This alternative seems unlikely, in view of the form of the phyllolepid element mentioned above, and is unparsimonious in requiring two reversals in evolution.

- (ii) Euarthroires are paraphyletic, the absence of the blade on the infragathal in some phlyctaenioids (e.g. *Holonema*, ?*Phlyctaenius*) is secondary, and the differentiated infragathal was inherited from the common ancestor of antiarchs and phlyctaenioids, which are sister groups.

Evidence against this proposal is evidence supporting euarthroiran monophyly. Of three characters proposed as euarthroiran synapomorphies by Miles and Young (1977, p. 134), only one can now be sustained (see Young 1979, p. 347; 1981*b*, p. 261; Young and Gorter 1981). This is the possession of two pairs of supragathals, but even this is not firmly established for actinolepids. An anterior supragathal is preserved *in situ* in *Kujdanowiaspis* (Stensiö 1963, pl. 62), and disarticulated elements which may be actinolepid posterior supragathals have been described by Denison (1958, 1960; see also Miles 1969, p. 145). However, better evidence is required to confirm that there is a posterior supragathal on the autopalatine in actinolepids. (Also of relevance in this connection are the position of the supragathals in phyllolepis—on the palatoquadrate or the braincase—and the number of supragathals in *Wuttagoonaspis*.) Another possible euarthroiran synapomorphy is proposed below (point *d*).

- (iii) Actinolepids and some phlyctaenioids are primitive in possessing an infragathal which lacks

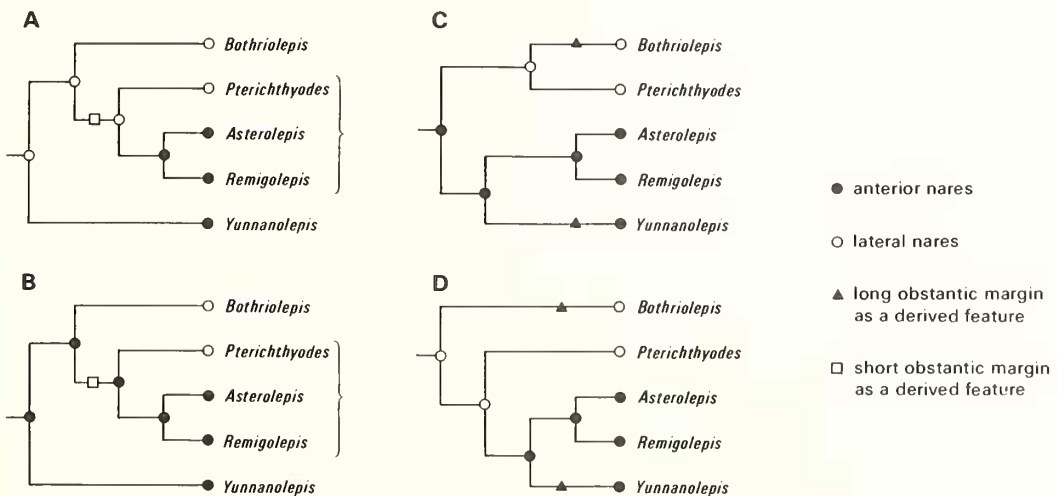
differentiated blade and biting portions. Resemblances between these and the infragnathal of phyllolepidids are symplesiomorphies. The differentiated infragnathal of brachythoracids and antiarchs arose independently in these two groups.

Assuming that the Euarthrodira is a monophyletic taxon, this hypothesis is to be preferred on the grounds of parsimony. If, however, actinolepidids are shown not to possess two pairs of supragnathals, then alternative (ii) would emerge as the preferred hypothesis. It also follows that the structure of the infragnathal cannot be used as evidence against Goujet's (in press) alternative hypothesis of antiarch relationships.

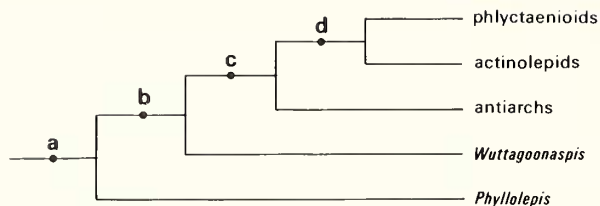
(c) *Submarginal articulation*. As noted above, the development of a dermal articulation between the submarginal plate and the skull-roof is a condition so far known only in *Bothriolepis*, and it thus has the status of an autapomorphy. However, further information on the presence or absence of this structure in other antiarchs thought to be closely related to *Bothriolepis* (e.g. *Dianolepis*, *Wudinolepis*, *Microbrachius*, *Hyrcanaspis*) should clarify relationships within the Bothriolepidoidei.

(d) *Quadrate and postsuborbital plate*. It is well known from the works of Stensiö (e.g. 1963, 1969) that the palatoquadrate in many advanced brachythoracids is represented only by autopalatine and quadrate ossifications. However, the notion that the intervening region may have been reduced to a ligamentous connection (e.g. Miles 1969, p. 144; 1971, p. 194; Ørvig 1975, p. 65) is no longer held (Miles and Dennis 1979, p. 49). On the evidence of *Holonema* (Miles 1971), *Dicksonosteus* (Goujet 1975), and *Buchanosteus* (Young 1979) it is clear nevertheless that there was a phyletic reduction and loss of perichondral ossification of the metapterygoid region within the Phlyctaenioidei.

In phlyctaenioids, and presumably in euarthrodirids generally, the quadrate is closely connected to the postsuborbital plate of the cheek. However, in the palatoquadrate of the palaeacanthaspid *Romundina*, Ørvig (1975, p. 65) has noted that the metapterygoid is perichondrally ossified on all sides at its posterior end, and neither the quadrate nor the postsuborbital plate is known. In view of the condition of the palatoquadrate in other gnathostomes, I am not convinced by Ørvig's suggestion that in *Romundina* the quadrate was a separate unit connected only by ligaments to the metapterygoid. Perhaps the mandibular joint had a high position on the non-preserved mesial surface of the palatoquadrate (see Ørvig 1975, pl. 2, fig. 5). Whatever the correct interpretation for *Romundina*, the apparently anomalous condition of the quadrate in relation to its dermal bone cover,



TEXT-FIG. 11. Alternative cladograms for some antiarchs, under an assumption that *Yunnanolepis* had anterior nares. In A and B the Asterolepidoidei (bracketed) are assumed monophyletic on the evidence of the short obstantic margin as a derived feature (synapomorphy). This feature is assumed primitive in C and D, making the asterolepidoids a paraphyletic group.



TEXT-FIG. 12. Interrelationships of some placoderms. Proposed synapomorphies, as discussed here, are: *a*, sliding dermal neck joint, posterior median ventral plate (if absent in petalichthyids), one pair of supragnathals. *b*, posterior lateral plate and pectoral fenestra in trunk-shield. *c*, long obstantic margin with prominent posterolateral corners on skull-roof, elongate rather than subovate submarginal plate, dermal prelateral and infraprelateral plates (or their homologues) in the cheek unit. *d*, second pair of supragnathals, quadrate fused to postsuborbital plate.

together with the fact that there was also no close association between the quadrate and an overlying dermal bone in *Bothriolepis*, points to the possibility that the postsuborbital/quadrate connection may be another synapomorphy defining euarthrodires. In addition, if the prelaterals and infraprelaterals of antiarchs are homologous with the postsuborbitals and infrapostsuborbitals of euarthrodires (Miles 1971; Denison 1978), then the possession of these bones may be proposed as another synapomorphy uniting these two groups.

(*e*) *Position of the nares in antiarchs.* To account for the presence of fine ornament in the preorbital depression I suggested above that the nares in *Yunnanolepis* opened laterally. This was also the opinion of Zhang Miman (1980), although in other respects (position of nasal capsules, etc.) our interpretations of the nasal region differ considerably. Conversely Zhang Guorui (1978) proposed that in *Yunnanolepis* the nares opened anteriorly as in *Remigolepis* (e.g. Stensiö 1948, fig. 16) and *Asterolepis* (e.g. Lyarskaya 1981, fig. 67). It is of significance, however, that in *Pterichthyodes* and probably *Gerdalepis* (Gross 1941; Stensiö 1948; Hemmings 1978) the rostral plate is developed like that of *Bothriolepis*, with lateral notches for the nares bounded anteriorly by a prenasal division of the plate. In a phylogenetic context this character distribution can be interpreted in several ways, depending on whether the asterolepidoid antiarchs are regarded as monophyletic or paraphyletic.

Young and Gorter (1981) suggested that the short obstantic margin facing posteriorly with posterolaterally extended postmarginal plates was an asterolepidoid synapomorphy, and that the group was monophyletic. If the nares opened anteriorly in *Yunnanolepis*, this would require either that the condition developed independently of that seen in *Asterolepis* and *Remigolepis* (text-fig. 11A), or that it was the primitive antiarch condition, which was separately lost in *Bothriolepis* and *Pterichthyodes* (text-fig. 11B). Both alternatives are less parsimonious than the assumption that in *Yunnanolepis* the nares were laterally placed, this being the primitive condition for antiarchs generally.

On the other hand, if the asterolepidoid antiarchs were assumed to be paraphyletic, the interpretation of *Yunnanolepis* as having anteriorly opening nares could be explained either as the primitive condition for antiarchs, which was lost in the common ancestor of *Pterichthyodes* and *Bothriolepis* (text-fig. 11C), or as a unique specialization of *Asterolepis*, *Remigolepis*, and *Yunnanolepis* (text-fig. 11D). However, under neither interpretation can the similarities in the obstantic margin and configuration of the postmarginal plate in *Bothriolepis* and *Yunnanolepis* be adequately explained. This must be the derived condition under this interpretation (since the other state of this character, as developed in *Asterolepis* and *Remigolepis*, is assumed to be sympleisomorphic) and in both schemes is independently acquired (text-fig. 11C, D). On the grounds of parsimony therefore it

can be concluded that laterally opening nares, as in *Bothriolepis*, was the primitive antiarch condition, and that the anterior position of the nasal openings in *Asterolepis* and *Remigolepis* is a synapomorphy of these genera. This is consistent with the observation that in other placoderms with ventral nares these are also directed more or less laterally (e.g. Stensiö 1963, figs. 10, 17). It can be predicted therefore that better material of *Yunnanolepis* will demonstrate that this form also had the primitive arrangement of lateral nares.

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REFERENCES

- DENISON, R. H. 1958. Early Devonian fishes from Utah. 3, Arthrodira. *Fieldiana, Geol.* **11**, 461–551.
 ——— 1960. Fishes of the Devonian Holland Quarry Shale of Ohio. *Ibid.* 555–613.
 ——— 1975. Evolution and classification of placoderm fishes. *Breviora*, **432**, 1–24.
 ——— 1978. *Placodermi Handbook of Paleichthyology, volume 2*. H.-P. SCHULTZE (ed.). Gustav Fisher Verlag, Stuttgart, 128 pp.
 DENNIS, K. D. and MILES, R. S. 1979a. A second eubrachythoracid arthrodire from Gogo, Western Australia. *Zool. Jl Linn. Soc.* **67**, 1–29.
 ——— 1979b. Eubrachythoracid arthrodires with tubular rostral plates from Gogo, Western Australia. *Ibid.* 297–328.
 ——— 1980. New durophagous arthrodires from Gogo, Western Australia. *Ibid.* **69**, 43–85.
 ——— 1981. A pachyosteoromorph arthrodire from Gogo, Western Australia. *Ibid.* **73**, 213–258.
 ——— 1982. A eubrachythoracid arthrodire with a snub-nose from Gogo, Western Australia. *Ibid.* **75**, 153–166.
 ——— 1983. Further eubrachythoracid arthrodires from Gogo, Western Australia. *Ibid.* **77**, 145–173.
 GARDINER, B. G. and BARTRAM, A. W. H. 1977. The homologies of ventral cranial fissures in osteichthyans. In ANDREWS, S. M., MILES, R. S. and WALKER, A. D. (eds.). *Problems in vertebrate evolution* 227–245. Academic Press, London.
 ——— and MILES, R. S. 1975. Devonian fishes of the Gogo Formation, Western Australia. *Colloques int. Cent. Natn. Rech. Scient.* **218**, 73–79.
 GOUJET, D. 1972. Nouvelles observations sur la joue d'*Arctolepis* (Eastman) et d'autres Dolichothoraci. *Annls Paléont.* **58**, 3–11.
 ——— 1975. *Dicksonosteus*, un nouvel arthrodire du Dévonien du Spitsberg. Remarques sur le squelette viscéral des Dolichothoraci. *Colloques int. Cent. Natn. Rech. Scient.* **218**, 81–99.
 ——— (in press). Placoderm interrelationships: a new interpretation, with a short review of placoderm classifications. *Proc. Linn. Soc. New South Wales*, **107**.
 GROSS, W. 1941. Neue Beobachtungen an *Gerdalepis rhenana* (Beyrich). *Palaeontographica*, A **93**, 193–214.
 HEINTZ, A. 1933. Some remarks about the structure of *Phlyctaenaspis acadica* Whiteaves. *Norsk geol. Tidsskr.* **14**, 127–44.
 HEMMINGS, S. K. 1978. The Old Red Sandstone antiarchs of Scotland: *Pterichthyodes* and *Microbrachius*. *Palaeontogr. Soc. (Monogr.)*, **131**, 1–64.
 JANVIER, P. and PAN JIANG 1982. *Hyrceanaspis bliecki* n.g. n.sp., a new primitive euantiarch (Antiarcha, Placodermi) from the Middle Devonian of northeastern Iran, with a discussion on antiarch phylogeny. *N. Jb. Geol. Paläont. Abh.* **164**, 364–392.
 LELIEVRE, H., JANVIER, P. and GOUJET, D. 1982. Les vertébrés Dévoniens de l'Iran central. IV: Arthrodires et ptyctodontes. *Géobios*, **14**, 677–709.
 LIU, T.-S. and P'AN, K. 1958. Devonian fishes from the Wutung Series near Nanking, China. *Palaeont. Sin.* **141**, 1–41. [In Chinese and English.]
 LONG, J. A. 1983. New bothriolepid fish from the Late Devonian of Victoria, Australia. *Palaeontology*, **26**, 295–320.
 ——— (in press). New phyllolepid fish from Victoria, and the relationships of the group. *Proc. Linn. Soc. New South Wales*, **107**.

- LYARSKAYA, L. A. 1981. *Baltic Devonian Placodermi Asterolepididae*. Zinatne, Riga, 152 pp. [In Russian with English abstract.]
- MILES, R. S. 1968. The Old Red Sandstone antiarchs of Scotland. Family Bothriolepididae. *Palaeontogr. Soc. (Monogr.)*, **122**, 1–130.
- 1969. Features of placoderm diversification and the evolution of the arthrodire feeding mechanism. *Trans. R. Soc. Edinb.* **68**, 123–70.
- 1971. The Holonematidae (placoderm fishes), a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Phil. Trans. R. Soc. B* **263**, 101–234.
- 1973. An actinolepid arthrodire from the lower Devonian Peel Sound formation, Prince of Wales Island. *Palaeontographica*, **A 143**, 109–18.
- 1977. Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *Zool. J. Linn. Soc.* **61**, 1–328.
- and DENNIS, K. 1979. A primitive eubrachythoracid arthrodire from Gogo, Western Australia. *Ibid.* **66**, 31–62.
- and WESTOLL, T. S. 1968. The placoderm fish *Coccosteus cuspidatus* Miller ex Agassiz from the Middle Old Red Sandstone of Scotland. Part I. Descriptive morphology. *Trans. R. Soc. Edinb.* **67**, 373–476.
- and YOUNG, G. C. 1977. Placoderm interrelationships reconsidered in the light of new ptyctodontids from Gogo, Western Australia. In ANDREWS, S. M., MILES, R. S. and WALKER, A. D. (eds.). *Problems in vertebrate evolution*. 123–198. Academic Press, London.
- NILSSON, T. 1941. The Downtonian and Devonian vertebrates of Spitsbergen. 7. Order Antiarchi. *Skr. Svalbard Ishavet*, **82**, 1–54.
- ORVIG, T. 1975. Description, with special reference to the dermal skeleton, of a new radotinid arthrodire from the Gedinian of Arctic Canada. *Colloques int. Cent. Natn. Rech. Scient.* **218**, 41–71.
- STENSJÖ, E. A. 1931. Upper Devonian vertebrates from East Greenland, collected by the Danish Greenland expedition in 1929 and 1930. *Meddr. Grönland*, **86**, 1–212.
- 1949. On the Placodermi of the Upper Devonian of East Greenland. 2. Antiarchi: subfamily Bothriolepinae. With an attempt at a revision of the previously described species of that family. *Ibid.* **139** (*Palaezool. Grönland*, 2), 1–622.
- 1963. Anatomical studies on the arthrodiran head. Part I. Preface, geological and geographical distribution, the organisation of the head in Dolichothoraci, Coccosteomorphi and Pachyosteomorphi. Taxonomic appendix. *K. Svenska Vetensk. Akad. Handl.* **9**, 1–419.
- 1969. Elasmobranchiomorphi Placodermata Arthrodires. In PIVETEAU, J. (ed.). *Traité de Paléontologie*, **4**, 71–692. Masson, Paris.
- TOOMBS, H. A. 1948. The use of acetic acid in the development of vertebrate fossils. *Museums J.*, **48**, 54–55.
- and RIXON, A. E. 1959. The use of acids in the preparation of vertebrate fossils. *Curator*, **2**, 304–312.
- YOUNG, G. C. 1979. New information on the structure and relationships of *Buchanosteus* (Placodermi, Euarthrodira) from the Early Devonian of New South Wales. *Zool. J. Linn. Soc.* **66**, 309–352.
- 1980. A new Early Devonian placoderm from New South Wales, Australia, with a discussion of placoderm phylogeny. *Palaeontographica*, **A 167**, 10–76.
- 1981a. Biogeography of Devonian vertebrates. *Alcheringa*, **5**, 225–243.
- 1981b. New Early Devonian brachythoracids (placoderm fishes) from the Taemas–Wee Jasper region of New South Wales. *Ibid.* **5**, 245–271.
- 1982. Devonian sharks from south-eastern Australia and Antarctica. *Palaeontology*, **25**, 817–843.
- (in press). Comments on the phylogeny and biogeography of antiarchs (Devonian placoderm fishes), and the use of fossils in biogeography. *Proc. Linn. Soc. New South Wales*, **107**.
- and GORTER, J. D. 1981. A new fish fauna of Middle Devonian age from the Taemas/Wee Jasper region of New South Wales. *Bull. Bur. Min. Res. Geol. Geoph.* **209**, 83–147.
- ZHANG GUORUI 1978. The antiarchs from the Early Devonian of Yunnan. *Vertebr. Palasiat.* **16**, 147–86. [In Chinese with English summary.]
- ZHANG MIMAN 1980. Preliminary note on a Lower Devonian antiarch from Yunnan, China. *Ibid.* **18**, 179–190. [In Chinese and English.]

G. C. YOUNG

Division of Continental Geology
Bureau of Mineral Resources
Geology and Geophysics
PO Box 378, Canberra City, ACT
Australia, 2601

ABBREVIATIONS USED IN TEXT-FIGURES

1	olfactory nerve	ifc	infraorbital sensory groove
2	approximate position of optic nerve	LA	lateral plate
ADL	anterior dorsolateral plate	laf	articular structure for dermal neck-joint
AVL	anterior ventrolateral plate	lat.p	lateral pit
a ₁ SM	anterior articular area for submarginal plate	lsg	main lateral line sensory groove
a ₂ SM	posterior articular area for submarginal plate	Mk	Meckel's cartilage
ad	anterior biting division of infragnathal	mf	dorsomesial face of non-biting division of infragnathal
ad ₁	anterodorsal process of submarginal plate	Nu	nuchal plate
ad ₂	posterior articular area for connection with skull	n	notch, possibly representing part of an articular area
a.m	thickened perichondral margin of area in contact with dermal bone	na	nasal opening
apl	unornamented lateral division of infra-prelateral plate	n.cav	nasal cavity
a.pr	anterior process of Meckel's cartilage	oa.AVL	overlap area for anterior ventrolateral
art	articular areas for orbital connection with braincase	oa.PrL	overlap areas for prelateral
art.md	articular surface for mandibular joint	ood	otico-occipital depression
art.op	articular area for opercular cartilage or epihyal	P	pineal plate
art.pb	articular area for palatobasal connection with braincase	PP	postpineal plate
art.v	ventral articular area, possibly for hyoid arch element	PM	postmarginal plate
a.sh	anterior shelf of Meckel's cartilage	PNu	paranuchal plate
aup	autopalatine part of palatoquadrate	PrL	prelateral plate
av	ventral articular area of submarginal plate	PrM	premedian plate
cd.art	articular condyle for mandibular joint	Py	infraprelateral plate
ch	ceratohyal	p.br	brachial process
cir	semicircular pit-line groove	pd	posterior non-biting division of infragnathal
cr ₁	prelateral crista	pe	pars pedalis of brachial process
cr ₂	postlateral crista	per	perichondral bone
cr.im	inframarginal crista	p.etho	postethmo-occipital section of endocranium
cr.pm	paramarginal crista	pin	pineal foramen
cr.pto	postorbital crista	plc	posterolateral corner of infragnathal
csf	central sensory line	pmm	posteromesial margin of posterior division of infragnathal
cv	cranial cavity	pnt	articular structure for dermal neck-joint
d.end	endolymphatic duct	p.pr	posterior process of suborbital plate
dent	denticulate biting margin	pq	palatoquadrate
df	dorsolateral face of non-biting division of infragnathal	pr.ant	antorbital process
eh	epihyal	pr.apo	anterior postorbital process
f.am	adductor fossa	pr.csp	craniospinal process
f.ax	axillary foramen	pr.dm	dorsomesial process of suborbital plate
fe.orb	orbital fenestra	pr.ect	ectethmoid process
fe.sorb	suborbital fenestra	pr.gl	glenoid process
fo.cu	cucullaris fossa	pr.ppo	posterior postorbital process
fo.md	mandibular muscle fossa	psoc	postsuborbital sensory groove
fp	funnel pit	R	rostral plate
f.vasc	foramina, probably vascular	r.epq	extrapalatoquadrate ridge
gr	groove, possibly for sensory pit-line	rh.cap	rhinocapsular section of endocranium
gr.ul	groove for upper lip	r.pq	dermal ridge supporting palatoquadrate
		SM	submarginal plate
		SO	suborbital plate
		sns	subnasal shelf
		soa	subobstantic area
		spio	foramina for spino-occipital nerves
		tlg	transverse lateral groove